CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY. XXXVIII.

NOTES ON THE GENUS CALOSTOMA.

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(WITH PLATE XIX)

THE genus Calostoma comprises a small group of gastromycetous fungi of peculiar habit which, though widely distributed geographically, are by no means well known as regards their developmental history. Even the commonest species, which is also the best known member of the group, and is met with not rarely in the whole eastern section of the United States, has never been obtained in a condition to show clearly the earlier phenomena connected with its spore formation. The lack of any definite information on this point has rendered the immediate affinities of the genus a matter of some uncertainty, and the present paper is offered as a slight contribution on the subject, based upon the examinition of material in unusually good condition collected by Dr. Thaxter in the vicinity of New Haven, Conn. The fact that this fungus passes its early stages just below the surface of the ground and is usually protruded only after the elements of the gleba, or spore bearing portion, have disappeared by absorption, renders it very difficult to procure in a young condition. The present material was obtained just as the plant was beginning to appear at the surface in a spot which had been marked during the previous season with this end in view. In addition to this young material just mentioned I have had access to specimens in Dr. Thaxter's herbarium, and the collections in the laboratory and herbarium of the Cryptogamic Department of Harvard University, including the collection of Dr. Curtis.

Although one of the American species of Calostoma was described as early as 1691, the first extended account of the

development of any member of the genus is that given by Fischer in 1884, in which the morphology and development of *C. cinnabarinum* are fully and correctly described. The material, however, on which this account was based does not seem to have been in condition to show the development of the gleba, except to a limited extent. The only remaining contribution of importance which relates to the morphology of the genus is that contained in the monograph published by Massee in 1888, where the development of *Calostoma cinnabarinum*, based upon specimens in the Kew Herbarium, is described in some detail. To this description we shall have occasion to refer presently.

At maturity *C. cinnabarinum*, which is the most common American species and may serve as a type for the whole genus, presents the appearance of an ochraceous globose body opening above by a stellate mouth guarded by toothlike valves, and extending below into a footstalk composed of anastomosing strands. The gleba lies at the center of the globose body, and is surrounded in its younger stages by four layers: (1) the volva, an outer gelatinous layer which soon disapppears; (2) the exoperidium, a layer just within the volva, also breaking away at an early stage; (3) the endoperidium, which is the external layer in older specimens; and (4) the spore sac containing the gleba.

Before passing to the development of the gleba, the other elements of the plant may be described briefly, further details concerning which may be sought in the accounts of either Fischer or Massee already referred to.

The volva, which envelops the fungus in its early stages, is composed of a homogeneous gelatinous mass arising from the gelatinification of the walls of a layer of hyphæ which are found imbedded in it and are developed in a radial direction from the exoperidium which lies next to it. When swollen by water, as it usually is in a state of nature, it constitutes a viscid jelly-like mass which soon becomes ruptured at the apex, partly through its own deliquescence, and partly by the protrusion of the inner elements up through it. At this stage it is separated from the

exoperidium except at the base, and sinks to the ground from its own weight (*fig. 4*), after which it deliquesces, and leaves but a slight trace of itself around the base of the footstalk and exoperidium.

The hyphæ found imbedded in the volva extend inward and form the exoperidium in which three rather distinct zones occur. The first or outermost is composed of branching hyphæ which run parallel with the periphery. In the middle zone the branching and anastomosing hyphæ run in a radial direction, becoming thicker as they extend inward, and soon pass over into the third zone in which the hyphæ are closely interlaced, and have their thick walls beset with numerous red granules. The hyphæ of the outer and middle zones lie imbedded in a mucilaginous substance which when dry gives the exoperidium a horny consistency, but when moistened swells considerably.

At first the hyphæ of the innermost layer of the exoperidium pass inward and are in connection with those of the endoperidium, but through the disintegration of the walls of the hyphæ forming the inner portion of the granular zone a separation soon takes place between these two layers. Owing partly to the distention of the endoperidium with its contained elements, and partly to the elongation of the footstalk in the region between the exoperidium and the endoperidium, the former is ruptured more or less irregularly around the base, at the same time splitting from below upward into numerous laciniæ, while not uncommonly a similar splitting may take place at the apex. As a result, the exoperidum becomes divided into numerous irregular segments which curl spirally either outward or inward, according as the mucilaginous substance in its outer zone is dry and contracted or moist and swollen. In this manner the exoperidium is finally removed by a process of peeling, so that in the more mature state little or none continues attached to the plant, the remainder lying about the base in the form of spirally twisted fragments.

The endoperidium is composed of thick walled closely interlaced hyphæ, and is of an extremely hard and enduring char-

acter, readily hibernating without injury. Its apex protrudes as an umbonate elevation which has from four to seven slits radiating from a center and dividing into a corresponding number of tooth-like valves, the inner surfaces of which are of a brilliant vermilion. The basal portion of the endoperidium forms the point of origin of the footstalk, which extends downward and breaks through the exoperidium in such a manner as to enclose completely patches of the red granular zone (*fig. 6, d*). Upon passing out of the endoperidium into the footstalk the hyphæ form themselves into anastomosing gelatinous strands (*fig. 6, b*) which give it the peculiar reticulate appearance seen in the mature specimens.

The tooth-like valves already mentioned open into the spore sac, which is composed of hyphæ somewhat smaller in diameter than those of the endoperidium. In the earlier stages the spore sac and endoperidium are in connection throughout, but a separation soon takes place, except at the apex in the region around the mouth where the connection between the two layers persists. After this separation the spore sac gradually contracts as the spores are discharged, so that a cavity is left between it and the endoperidium.

The hyphæ of the wall of the spore sac continue inward and form the gleba, which is of a yellowish color, and, when seen in cross section in its early stages, has a lobulated appearance, the cleft-like cavities between the lobules being traversed by loose strands of large brownish yellow branching hyphæ which form an irregular network (*fig. 5*). These hyphæ (*fig. 7*) are 3–4 μ thick, with frequent septa and clamp connections, and are marked with irregular transverse thickenings (*a*). They appear to have no connection with the fertile hyphæ; a fact which, together with the presence of the annular thickenings, would seem to indicate that they may represent a rudimentary capillitium, although I have not been able to find them after the spores arrive at maturity.

The fertile hyphæ are about 3 μ thick, much branched and bent and of a yellowish color. At an early period of their

development they are thickly beset with numerous small rounded wart-like protuberances, and also short secondary branches of a smaller diameter than the primary hyphæ (*fig. 8, b*). At this stage, also, numerous oblong cells are developed from the fertile hyphæ which give to the gleba a characteristic appearance. These cells (*fig. 8 a*), which are at first globose, but at maturity become slightly oblong, are found borne upon the primary hyphæ, either laterally or terminally, in the center of a cluster of secondary branches which grow up around them. At maturity they are easily detached and may be seen isolated and scattered in all directions in the gleba as spore-like bodies measuring from $4–7 \times 7–11 \mu$. It is probable that these are the cells to which Fischer (1884) refers as occurring between the hyphæ of the gleba. On the further development of the gleba these cells entirely disappear through absorption, while the secondary branches which surround them develop into hyphæ bearing the basidia. Before this takes place, however, the spore sac, with the exception of a small area at the apex, becomes separated from the endoperidium, thus greatly reducing the surface upon which the gleba can draw for nutriment. The fact that the oblong cells disappear soon after this separation takes place may perhaps indicate that their function is to serve as reservoirs of food for the later stages of the other elements of the gleba.

As has just been stated, after the disappearance of the oblong cells above described, the secondary hyphæ are found to have developed considerably, and at the ends of their numerous branches the basidia are borne. These hyphæ have by this time increased to the diameter of the primary hyphæ, and like them are beset with numerous wart-like protuberances. The basidia (*fig. 9*) are usually club shaped, but vary widely; oftentimes being very nearly cylindrical and of the same diameter as the hyphæ which bear them, and from which they are separated by a transverse septum. The spores, which at first are subglobose and later become ellipsoid and punctate, are borne laterally as well as terminally; being more or less evenly distributed over the whole surface of the basidium, as in Tulostoma. The number

occurring on a single basidium varies from five to ten or twelve. My material contained no specimens with the mature spores still *in situ;* but in that which I examined, although the spores were considerably advanced, there were no sterigmata.

In his monograph, already referred to, Massee describes and figures the basidia as "broadly obovate, measuring from 40–50 × 15–20 μ, and bearing five or sometimes six spores supported on minute wart-like prominences arranged in a circle around the apex." In my material, however, the position of the spores is very characteristic, and in no specimen which I examined were they in the least confined to the apex of the basidia, nor did they show any tendency to a circular arrangement in this region.

The fact that the spores are borne laterally upon the basidia in Calostoma seems to point at once to its affinity with Tulostoma, the only other gastromycete in which the spores are similarly borne. Fischer is of the opinion that the double peridium in Calostoma indicates its affinity with Geaster; a view also supported by Massee. The latter observer homologizes the external peridium of Geaster with the exoperidium and endoperidium of Calostoma, and the inner peridium of Geaster with the spore sac in Calostoma. He calls attention, however, to the wide difference which exists in the fact that in Geaster the inner peridium is confluent with the base of the outer peridium, while in Calostoma what he considers as the morphological equivalents of these two elements are confluent at the apex. The affinity of Calostoma with Tulostoma, however, seems to offer a more simple explanation of the facts. If we consider that the part of the peridium immediately surrounding the gleba in Tulostoma becomes differentiated to form the spore sac, but still remains attached to the outer shell of the peridium (endoperidium) at the apex, and that the rest of the peridium becomes differentiated into three layers (volva, exoperidium, and endoperidium), we see how readily the differences between the two genera may be explained. Both Calostoma and Tulostoma agree in being forced to the surface by the extension of a footstalk. In

Calostoma this footstalk is surrounded in its younger stages by the volva and exoperidium, and is plainly seen to arise from the endoperidium (*fig. 6*). In Tulostoma the footstalk is likewise surrounded in its younger stages by a portion of the peridium, which we may consider to be equivalent to the volva and exoperidium in Calostoma, and the inner region of the peridium from which the footstalk arises is probably the morphological equivalent of the endoperidium.

The similarity which exists between the basidia of the two genera is very close indeed, the greatest difference being that in the species of Calostoma under consideration the number of spores on a single basidium is considerably larger. Schroeter's original figure of the basidia of Tulostoma represents the spores with scarcely any sterigmata, and in his description he speaks of their nearly sessile character, so that the difference which exists in this respect is very slight.

Briefly stated, then, the evidence which seems to point to the affinity of Calostoma with Tulostoma rather than with Geaster, is found in the fact that both genera possess a form of basidium found in no other gastromycete, while the basidia of Geaster are entirely different; and that in explaining the differences which exist between Calostoma and Tulostoma by a simple process of evolution, no such obstacle has to be overcome as is found in the fact that, in Calostoma, the sporè sac and endoperidium are united at the apex, while in Geaster what Massee considers their morphological equivalents are united at the base.

The anomalous character of such a type of basidium in so highly developed a gastromycete, which finds its only parallel within the group in the four-spored basidia of Tulostoma, is a matter of some interest in connection with any attempt to draw comparisons between the typical basidiomycetes and the supposed transitional forms. In the present instance it must be admitted that (assuming the basidial nature of the sporophores of Pilacre) the peculiar basidia just described, together with the number, position and sessile character of the spores, would render comparatively easy the steps from the angiocarpous Pro-

tobasidiomycetes of Brefeld's "system" to the typical Gastromycetes.

From a systematic point of view the American species of Calostoma are not without a certain interest, especially in connection with the uncertainty which has prevailed concerning the distinctions existing between *C. cinnabarinum* and *C. lutescens*. The earliest reference to either of these species is, so far as can be ascertained, that which is made by Plukenet in his *Phytographia* (1691), where, as pointed out by Farlow (1887), a fungus, probably referable to *C. cinnabarinum*, is figured and briefly described as follows: "Fungus pulverulentus virginianus caudice corallino topiario opere contorto." More than a century later Persoon (1809) described and figured one of the American forms under the name of *Scleroderma callostoma*, remarking that if many species with a similarly shaped mouth were found a new genus should be formed, and later in the same year Desvaux (1809) established this new genus, giving it the name of Calostoma, and describing the only American species then known as *C. cinnabarinum*. In 1811 Bosc again described it as *Lycoperdon heterogeneum*, probably not having seen either Persoon's or Desvaux's description, as he makes no reference to them. Like Persoon, Bosc states that it should form a new genus, and in 1817 Nees von Esenbeck, who was also evidently ignorant of the description of the two last named authors, for a second time places it in a new genus, calling it *Mitremyces heterogeneus*. In 1825 Edward Hitchcock in an article on *C. cinnabarinum* in *Am. Jour. Sci.* calls it *Gyropodium coccineum*, a name which he ascribes to Schweinitz, but evidently upon no published authority. Later Corda in 1842 retains both the generic names of Calostoma and Mitremyces, referring *C. cinnabarinum* to the former and *C. lutescens* to the latter; while lastly in 1888 all the species of the genus were returned by Massee to the older name of Calostoma.

The genus contains ten species, which are widely distributed; occurring in America, Australia, southern Asia, and the Malay Archipelago.

The similarity in the appearance of *C. lutescens* and *C. cinnabarinum* has led to the confusion which has existed concerning their distinctions. Schweinitz in 1822 described a form from Carolina as *M. lutescens* and later in 1831 a second species as *M. cinnabarinum*. Sprengel (1827), Fries (1849), and Nees, Henry, and Bail (1837) all give *M. lutescens* as the only American species, but Corda, as we have just seen, gives also *Calostoma cinnabarinum*, without being aware of its generic connection with *Mitremyces lutescens*. Massee in his monograph states that owing to the considerable variations in size, color and form which *C. cinnabarinum* presents he is of the opinion that the *Mitremyces lutescens* of Schweinitz is but a young condition of his *M. cinnabarinum*, and unites the two under this name. The only reference made to the shape of the spores of *M. lutescens* by the early observers is found in the description of Corda, who states that they are globose. *Calostoma cinnabarinum*, on the other hand, as is well known, has ellipsoid punctate spores. Among the specimens contained in the Curtis collection and labeled *M. lutescens* are two examples, however, one from Alabama (coll. *Peters*), the other from West Virginia (coll. *A. H. Curtiss*), which agree with Corda's description in possessing globose spores. They further differ from *C. cinnabarinum* in having a longer footstalk, the gelatinous strands of which are finer and more closely woven, while the color is of a more uniform pale yellowish. The length of the footstalk (*fig. 1*) was as much as 9^{cm}, although part of it had evidently been broken off at the base, and in a fresh state it might have been even longer.

These two dried specimens were the only material of *C. lutescens* which I was able to examine, but they indicate that Massee was in error in considering the species identical with *C. cinnabarinum*, and that, while it is probably the globose spored form to which Schweinitz gave the name of *M. lutescens*, it is, with little doubt, the form which Corda describes by that name. The "*M. lutescens*" from Ceylon described by Massee as *C. Berkeleyi* is identical with the American form as far as concerns the character and measurements of the spores. The habit,

however, as represented in Massee's figure does not present the same peculiarities which appear to distinguish our species.

Another small species from South Carolina was first described in 1857 by Berkeley as *M. Ravenelii*. It is smaller than the other two American forms, and further differs from them in the fact that its exoperidium often remains attached to the endoperidium in the form of wart-like protuberances.

Three American species may then be distinguished as follows:

CALOSTOMA CINNABARINUM Desv. *Plate XIX, figs. 3–10.*

Fungus pulverulentus Plukenet, Phytographia *pl. 184. fig. 5.* 1691.

Calostoma cinnabarinum Desvaux, Jour. de Bot. **2**: 94. 1809.

Scleroderma calostoma Persoon in Desv., Jour. de Bot. **2**: 15. *pl. 2. fig. 2.* 1809.

Lycoperdon heterogeneum Bosc, Mag. Ges. Nat. Fr. **5**: 87. *pl. 6. fig. 10 a, b.* 1811.

Lycoperdon calostoma Poir. Encycl. Suppl. **5**: 476. 18—.

Mitremyces heterogeneus Nees, Syst. der Pilze und Schwämme 136. *pl. 11. fig. 129a.* 1817.

Gyropodium coccineum Hitchcock, Am. Jour. Sci. **9**: 56. *pl. 3.* 1825.

Mitremyces cinnabarinum Schweinitz, Syn. Fung. Amer. Bor. in Amer. Phil. Soc. 255. no. 2244. 1831.

Mitremyces lutescens Ell. & Ev. Fung. Columb. 799, N. A. F. 727; Rav. Fung. Car. **1**: 76.

Exoperidium vermilion within, breaking at base, sometimes at apex also, into laciniæ. Endoperidium ochraceous, often slightly vermilion; ostiolum vermilion, teeth 4–7. Footstalk reddish brown or brownish, 1–6^{cm} long by .75–3^{cm} wide. Spores elliptic-oblong, echinulate or punctate, pale ochre yellow, 15–18 × 8–10μ.

Eastern part of the United States: Massachusetts (*Faxon*), Pennsylvania (*Schw.*), Carolina (*Rav.*), Texas (*Drum.*), Ohio (*Morgan*), Tennessee and Connecticut (*Thaxter*).

It makes its appearance above ground towards the end of July, and is more commonly found growing in rather moist situations along the banks of streams in woods, sometimes occurring in dryer localities. Although under the ordinary powers of the microscope the spores appear echinulate, examination with higher magnification shows them to be rather punctate, the points corresponding to striations in the spore wall as is shown in *fig. 10a*. The surface

of the spore may also be covered with a flaky incrustation present in small irregular patches as in *b*.

CALOSTOMA LUTESCENS (Schwein.) *Plate XIX, figs. 1, 2.*

Mitremyces lutescens Schweinitz, Syn. Car. p. 60 no. 345. 1822; Corda, Anleitung, 79, *pl. D. fig. 41, nos. 15–17.* 1842.

Calostoma cinnabarinum Massee *pro parte*, Annals of Botany 2: 42. 1888.

Exoperidium light yellowish. Endoperidium smooth, yellowish, ostiolum pale vermilion within. Footstalk longer, its strands somewhat finer than in the last species, yellowish, 7–9^{cm} long by .75–2^{cm} wide. Spores globose, verrucose, 7–9μ.

Alabama (*Peters*), West Virginia (*A. H. Curtiss*).

Several specimens in the Curtis collection are labeled *M. lutescens*, only two of which appear really to belong to this species. Although the age of the specimens does not admit of any accurate description of their gross appearance, they seem to differ from *C. cinnabarinum* in their pale yellowish color and longer more highly developed footstalk, which appears to attain a greater length than is ever seen in the last mentioned species. The endoperidium, when it still remains, is yellowish within and without, a fact which may be due to its being faded with age. The inner faces of the teeth, however, have a distinct vermilion tint. The round verrucose spores which vary greatly in size at once distinguish the species from *C. cinnabarinum*, and as already mentioned coincide with the description given by Corda.

CALOSTOMA RAVENELII (Berk.) Massee.

Mitremyces Ravenelii Berkeley, Trans. Linn. Soc. 22: 130. *pl. 25 B.* 1857.
Calostoma Ravenelii Massee, Annals of Botany 2: 25. 1888.

Smaller than last two species, the exoperidium remaining attached to the ochraceous endoperidium in the form of irregular warts or scales. Footstalk short. Spores elliptic oblong, smooth.

North and South Carolina, "upland and deadwood" (*Curtiss*).

Although Morgan considers the species as synonymous with *M. lutescens*, it appears to differ in its uniformly smaller size and ill-developed footstalk, as well as by its different color and the peculiar mode of rupture of its exoperidium, which remains attached in scale-like fragments all over the surface of the endoperidium, the Herb. Curtis specimens agreeing in this respect with those of Berkeley as figured by Massee, while the smaller smooth spores described and figured by the last named writer would constitute an additional point of difference.

In closing I wish to take this opportunity to acknowledge my indebtedness to Dr. Thaxter for the very great assistance which he has rendered me in preparing this paper.

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EXPLANATION OF PLATE XIX.

Calostoma lutescens.

FIG. 1. Gross habit drawn from dried specimens.

FIG. 2. Three spores showing ordinary variation in size. Obj. J. oc. 4.

Calostoma cinnabarinum.

FIG. 3. Gross habit after disappearance of volva and exoperidium; fragments of the latter (*c*) still remaining; *a*, mouth; *b*, endoperidium; *d*, footstalk.

FIG. 4. Specimen from which the volva has been partly removed through deliquescence. The exoperidium is shown splitting from the base upward.

FIG. 5. Section through a portion of the gleba showing the rudimentary capillitium (*a*) extending inward from the wall of the spore sac (*b*) and forming loose strands between the lobules of fertile hyphæ (the latter are not shown in the figure). Obj. A. oc. 4, Zeiss.

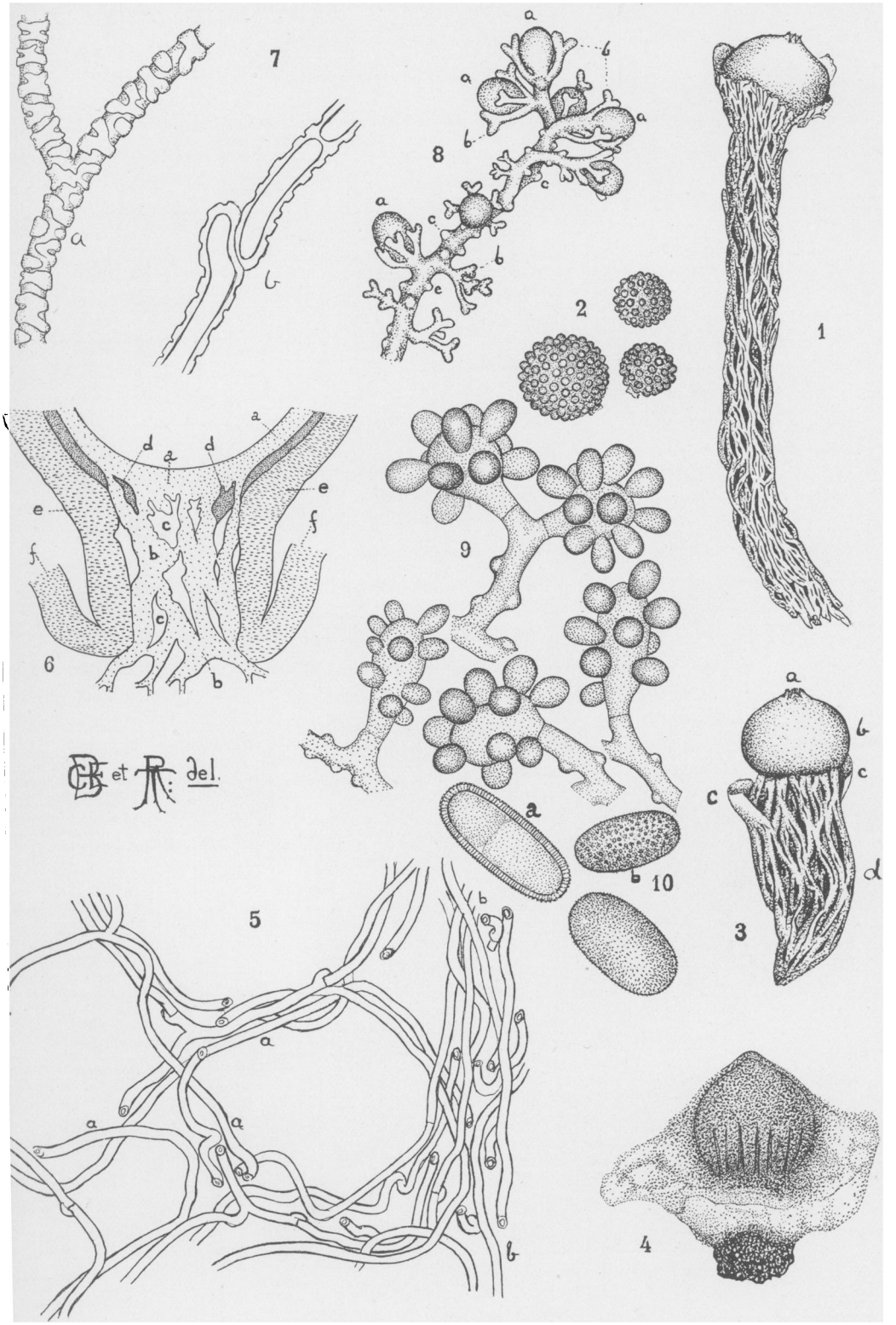
FIG. 6. Semi-diagrammatic section through the base of a young specimen; *a*, endoperidium extending downward to form the strands of the footstalk (*b*), which encloses cavities (*c*) and portions of the granular layer of the exoperidium at *d*; *e*, exoperidium; *f*, volva.

FIG. 7. Rudimentary capillitium showing superficial thickenings (*a*), clamp connection and septum (*b*).

FIG. 8. Portion of primary hypha showing the oblong cells (*a*) and secondary hyphæ (*b*), which later bear the basidia; *c*, wart-like projections from primary hypha. $\frac{1}{12}$ oil, oc. 4.

FIG. 9. Five basidia with developing basidiospores. Obj. J. oc. 4.

FIG. 10. Three spores; *a*, optical section showing striation of wall. Obj. J. oc. 4.



BURNAP on CALOSTOMA.